The Veliger 44(4):398–406 (October 1, 2001)

THE VELIGER

NOTES, INFORMATION & NEWS

The Early Veliger Larvae of *Aegires albopunctatus* (Nudibranchia: Aegiridae), with Morphological Comparisons to Members of the Notaspidea

Jeffrey H. R. Goddard
Marine Science Institute, University of California,
Santa Barbara, California 93106, USA

Introduction

Most opisthobranchs hatch from their egg masses as planktotrophic veliger larvae with a clear unsculptured shell, an operculum, a thin foot lacking a propodium, and no eyespots (Thompson, 1976; Bonar, 1978; Todd, 1981; Hadfield & Switzer-Dunlap, 1984; Goddard, 1992, in press). As part of an ongoing survey of developmental mode in opisthobranchs from the northeastern Pacific Ocean, I examined the previously undescribed hatching larvae of the nudibranch *Aegires albopunctatus* MacFarland, 1905. These larvae are planktotrophic, but differ from other opisthobranchs with this mode of development in almost all of the characters listed above. In this note, I describe these unusual larvae and compare them to both the later stage larvae of *Aegires punctilucens* (d'Orbigny, 1837) described by Thiriot-Quiévreux (1977) and to the planktotrophic larvae of some notaspidean opisthobranchs that also lack an operculum throughout their ontogeny. *Aegires albopunctatus* ranges from British Columbia, Canada to Baja California, Mexico (McDonald, 1983; Behrens, 1991) and is the only representative of the family Aegiridae known from the northeastern Pacific Ocean.

Three specimens of *Aegires albopunctatus,* 10–12 mm long, were collected subtidally from Naples Reef, Santa Barbara County in May 2000 by Shane Anderson, and held in a 100 ml jar of filtered seawater at 14–17°C until they laid egg masses. I examined the newly laid egg masses using a compound microscope equipped with an ocular micrometer, measured the diameter of the zygotes, and then transferred the egg masses to separate vials. I changed the water in these vials daily, and examined the egg masses daily until the veligers hatched. I then examined, measured, and photographed the live hatching veligers using a compound microscope equipped with a 35 mm camera. I did not attempt to rear the larvae beyond hatching. After obtaining the above egg masses, I preserved the adults and deposited them as voucher specimens in the Department of Invertebrate Zoology at the Santa Barbara Museum of Natural History (catalogue number 345473).

Results and Discussion

Aegires albopunctatus laid white egg ribbons, 2 mm wide, in a loose spiral of one and a third turns. The mean diameter of the uncleaved eggs was 98.0 μm (SD = 1.09 μm, n = 10), considerably less than the range of 107–120 μm reported by Strathmann (1987:283) for this species from the San Juan Islands, Washington. This is probably not enough of a difference in diameter to indicate intraspecific variability in mode of development, or poecilogony (e.g., see Krug, 1998). However, larvae obtained from the San Juan Islands should be examined for potential morphological differences from those described below. At 14–17°C, the eggs from the Santa Barbara specimens took 12.5 days to develop into hatching veliger larvae with typical coiled shells (type 1 of Thompson, 1961, and Strathmann, 1987:271), averaging 153.7 μm in length (SD = 6.40 μm, n = 5).

The hatching larvae of *Aegires albopunctatus* (Figure 1) had a strongly bilobed velum measuring up to 225 μm wide across the two lobes, and a mantle folded over the edge of the shell aperture. They were largely transparent and lacked significant yolk reserves. Their foot lacked a propodium. This set of traits unequivocally indicates a planktotrophic mode of larval development (Thompson, 1967, 1976; Bonar, 1978). However, the larvae of *A. albopunctatus* differ from the hatching planktotrophic larvae of most other species of opisthobranchs in four significant ways. (1) They lacked an operculum, had an unusually large velum, and were incapable of withdrawing completely into their shells. If disturbed, the larvae stopped swimming, folded the two lobes of the velum together like the wings of a butterfly, and withdrew only slightly into the shell. Thiriot-Quiévreux (1977) described a similar response in slightly older larvae of *A. punctilucens,* which also lack an operculum and possess a similarly large velum. (2) Although the foot of *Aegires albopunctatus* lacked a propodium, it was significantly longer, thicker, and more inflated than those of other planktotrophic opisthobranch larvae (Figure 1). It was also drawn laterally into rounded lobes that overlapped slightly the sides of the shell, and contained distally an unusual concentration of opaque white, spherical inclusions (Figure 1). These inclusions measured 10 μm in diameter and may constitute some kind of pedal gland. (3) The inner whorl of the shell had a translucent brown tinge and a wavy sculpture reminiscent of that found in patellogastropods (see Amio, 1963). (4) The veliger larvae of *A. albopunctatus* hatched with dark eyespots. Eyespots are known in the hatching planktotrophic larvae of many nu-

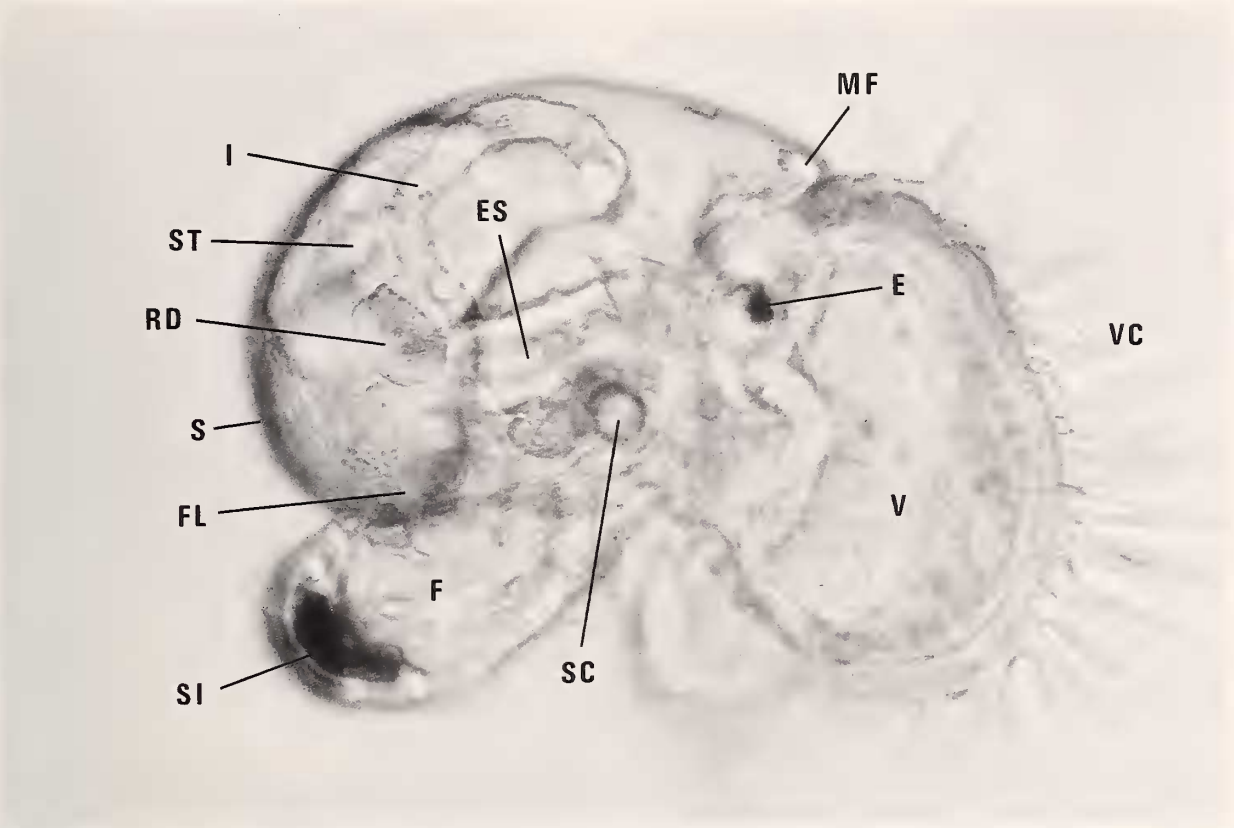

Figure 1. Live, newly hatched veliger larva of *Aegires albopunctatus,* right lateral view. The shell of this specimen was 155 μm long. The left digestive diverticulum is the large, rounded body ventral to and behind (in this view) the stomach. Bright field microscopy. Key: E, eyespot; ES, esophagus; F, foot; FL, lateral foot lobe; I, intestine; MF mantle fold; RD, right digestive diverticulum; S, shell; SC, statocyst; SI, opaque spherical inclusions; ST, stomach; V, velum; VC, velar cilia.

dibranchs with egg-shaped, type 2 larval shells (Goddard, 1991), but are rare in the hatching planktotrophic larvae of other opisthobranchs (Thompson, 1976; Todd, 1981; Hadfield & Switzer-Dunlap, 1984; Goddard, 1992, in press).

The hatching larvae of *Aegires albopunctatus* resemble older larvae of *A. punctilucens* in the lack of an operculum and in the size of the velum relative to the size of the shell and body (Thiriot-Quiévreux, 1977). Thiriot-Quiévreux (1977) worked only with samples collected from plankton and did not describe the hatching larvae of *A. punctilucens,* so it is unknown if these larvae also hatch with eyespots. The earliest larvae Thiriot-Quiévreux (1977) examined had a flat-soled foot with an obvious propodium (see her figure 1a), but the morphology of the foot at hatching in *A. punctilucens* is not known.

Aegires punctilucens is the only benthic opisthobranch known to cast its shell during the larval stage (gymnosome pteropods, which are planktonic as adults, cast their thimble-shaped shell white still veligers [Lebour, 1931]). It then develops a juvenilelike body with rhinophores, large foot, and a highly spiculate dorsum while still in possession of a velum and swimming (Thiriot-Quiévreux, 1977). The large velum of this species is therefore likely to be an adaptation for carrying the extra weight of the developing juvenile. The similarities between the shelled larvae of *A. punctilucens* and those of hatching *A. albopunctatus* suggest that the latter may undergo a similar larval development and two-stage metamorphosis.

The only other opisthobranchs with planktotrophic development known to hatch with eyespots and to lack an operculum throughout their ontogeny are the pleurobranchacean notaspideans *Pleurobranchus* sp. from Hawaii (Ostergaard, 1950:107), *Pleurobranchaea japonica* Thiele, 1925 from Japan (Tsubokawa & Okutani, 1991), *Berthella californica* (Dall, 1900) from Oregon (Goddard, in press), and *Berthellina engeli* Gardiner, 1936, from Santa Barbara, California (personal observations). Like *Aegires punctilucens* and *A. albopunctatus,* the larvae of these species have a large velum that prevents withdrawal of the body into the shell, especially as the rest of the body grows. As in *Aegires,* the mantle of these notaspideans grows significantly during the veliger stage. However, in the pleurobranchaceans it grows to completely cover the

shell, which is retained through the benthic juvenile stage (Tsubokawa & Okutani, 1991). The pleurobranchaceans also develop rhinophores while still larvae (Tsubokawa & Okutani, 1991), but these have the longitudinal slit characteristic of the order (Willan, 1987). In addition, notaspidean larvae possess pigmented mantle organs on the right side of the body, a trait unknown in nudibranch larvae (Robertson, 1985; Goddard, 1984:147, in press).

The development and elaboration of the mantle of *Aegires* and pleurobranchacean notaspideans during their larval stage appears to have necessitated the increased locomotive power of an enlarged velum. These changes, in turn, have precluded the withdrawal of the velum and foot into the shell, and appear to have rendered the operculum useless. Why these species also hatch with eyespots, when the vast majority of planktotrophic opisthobranchs do not, remains a mystery.

Literature Cited

Amio, M. 1963. A comparative embryology of marine gastropods, with ecological considerations. The Journal of the Shimonoseki University of Fisheries 12:15–144.

Behrens, D. W. 1991. Pacific Coast Nudibranchs. Sea Challengers: Monterey, California. 107 pp.

Bonar, D. B. 1978. Morphogenesis at metamorphosis in opisthobranch molluscs. Pp. 177–196 in F. S. Chia & M. E. Rice (eds.), Settlement and Metamorphosis of Marine Invertebrate Larvae. Elsevier/North-Holland Biomedical Press: New York.

Goddard, J. H. R. 1984. The opisthobranchs of Cape Arago, Oregon, with notes on their biology and a summary of benthic opisthobranchs known from Oregon. The Veliger 27: 143–163.

Goddard, J. H. R. 1991. Unusually large polar bodies in an aeolid nudibranch: a novel mechanism for producing extraembryonic yolk reserves. Journal of Molluscan Studies 57 (4, supplement):143–152.

Goddard, J. H. R. 1992. Patterns of development in nudibranch molluscs from the northeast Pacific Ocean, with regional comparisons. Ph.D. Dissertation, University of Oregon, Eugene, Oregon. 237 pp.

Goddard, J. H. R. In press. Mollusca: Gastropoda. Chapter in A. L. Shanks (ed.), An Identification Guide to the Larval Marine Invertebrates of the Pacific Northwest. Oregon State University Press: Corvallis, Oregon

Hadfield, M. G. & M. Switzer-Dunlap. 1984. Opisthobranchs. Pp. 209–350 in A. S. Tompa, N. H. Verdonk & J. A. M. van den Biggelaar (eds.), The Mollusca. Vol. 7, Reproduction. Academic Press: New York.

Krug, P. J. 1998. Poecilogony in an estuarine opisthobranch: planktotrophy, lecithotrophy, and mixed clutches in a population of the ascoglossan *Alderia modesta*. Marine Biology 132:483–494.

Lebour, M. V. 1931. *Clione limacina* in Plymouth waters. Journal of the Marine Biological Association of the United Kingdom 17:785–795.

McDonald, G. R. 1983. A review of the nudibranchs of the California coast. Malacologia 24:114–276.

Ostergaard, J. M. 1950. Spawning and development of some Hawaiian marine gastropods. Pacific Science 4:75–115.

Robertson, R. 1985. Four characters and the higher category systematics of gastropods. American Malacological Bulletin, Special Edition No. 1:1–22.

Strathmann, M. F. 1987. Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast. University of Washington Press: Seattle, Washington. 670 pp.

Thiriot-Quiévreux, C. 1977. Véligère planctotrophe du doridien *Aegires punctilucens* (D'Orbigny) (Mollusca: Nudibranchia: Notodorididae): description et métamorphose. Journal of Experimental Marine Biology and Ecology 26:177–190.

Thompson, T. E. 1961. The importance of the larval shell in the classification of the Sacoglossa and Acoela (Gastropoda, Opisthobranchia). Proceedings of the Malacological Society of London 34:233–238.

Thompson, T. E. 1967. Direct development in the nudibranch *Cadlina laevis*, with a discussion of developmental processes in Opisthobranchia. Journal of the Marine Biological Association of the United Kingdom 47:1–22.

Thompson, T. E. 1976. Biology of Opisthobranch Molluscs. Vol. 1. Ray Society: London.

Todd, C. D. 1981. The ecology of nudibranch Mollusca. Oceanography and Marine Biology, an Annual Review 19:141–234.

Tsubokawa, R. & T. Okutani. 1991. Early life history of *Pleurobranchaea japonica* Thiele, 1925 (Opisthobranchia: Notaspidea). The Veliger 34:1–13.

Willan, R. 1987. Phylogenetic systematics of the Notaspidea (Opisthobranchia) with reappraisal of families and genera. American Malacological Bulletin 5:215–241.

Further Spread of the Introduced Decollate Snail, *Rumina decollata* (Gastropoda: Pulmonata: Subulinidae), in California, USA

Jeff Tupen

Morro Group, Inc., 1422 Monterey Street, Suite C200, San Luis Obispo, California 93401, USA

and

Barry Roth

Santa Barbara Museum of Natural History, 2559 Puesta Del Sol Road, Santa Barbara, California 93105, USA

This note reports the occurrence of established colonies of the non-native, terrestrial decollate snail, *Rumina decollata* (Linnaeus, 1758), in San Luis Obispo County, central California, and on San Nicolas Island, Ventura County, southern California. This species is banned from San Luis Obispo County by California law. *Rumina decollata* is a detritivore, herbivore, and facultative predator on other snails. Its presence in San Luis Obispo County may pose a threat to the Morro shoulderband snail, *Helminthoglypta walkeriana* (Hemphill, 1911), which is listed as endangered under the U.S. Endangered Species Act. Its presence on San Nicolas Island may harm the unique indigenous snail fauna of that island.

Rumina decollata (Figure 1) is native to the Mediterranean region of southern Europe and North Africa. It was first reported in the eastern United States in 1813 and in California in 1966 (Fisher, 1966; Fisher et al., 1980),